

REGENERATION OF THE INHALANT SIPHON OF *MESODESMA MACTROIDES* (DESHAYES, 1854) (MOLLUSCA: BIVALVIA)

Jesús D. Nuñez^{1, 2}, Marcelo A. Scelzo^{1, 2} & Maximiliano Cledón^{1, 2*}

INTRODUCTION

Infaunal biota faces the compromise between predation avoidance and contact with the surface to maintain such biological functions as feeding, excretion, respiration, and reproduction. A compromise is attained, in the case of bivalves, through the siphons, optimising the interaction with the superficial environment (McLachlan et al., 1995). However, the exposure of these structures can enhance the risk for predation, making infaunal bivalves more vulnerable to tissue cropping by browsing feeders, such as crabs (Kamermans & Huitema, 1994), pelagic juvenile flatfishes (Trevallion et al., 1970) and birds (Zwarts, 1986). Siphon cropping has been reported for several bivalve species (Trevallion, 1971; Hodgson, 1982; Peterson & Quammen, 1982; Zwarts, 1986).

Many bivalve species have siphons, which can be seen as a renewable resource, if they regenerate after cropping (Penchaszadeh, 1983; Pekkarinen, 1984; Riera, 1995; Luzzatto & Penchaszadeh, 2001). Such processes function as secondary production to higher trophic levels in food webs. However, regeneration occurs at the expense of somatic growth and reproduction, affecting fitness (Geller, 1990; Peterson & Quammen, 1982; Kamermans & Huitema, 1994; Irlandi & Mehlich, 1996).

The yellow clam *Mesodesma mactroides* is an intertidal suspension-feeder, well adapted to its life mode (Narchi, 1981). It is an endemic infaunal inhabitant of the Atlantic coast of South America from southern Brazil to northern Patagonia, Argentina (Castellanos, 1970). In Argentina, its populations occur over 375 km of sandy beaches.

The inhalant siphon of *M. mactroides* is fringed with three series of unpigmented tentacles. The innermost series comprises eight tentacles, the largest and most ramified of the crown, which are directed inward as water enters the mantle cavity. These primary tentacles

are interspersed with by small foliose tentacles, which are also inwardly directed, so that the inhalant aperture is, in effect, covered by a coarse sieve when active (Narchi, 1981).

In this study, we conducted the regeneration process of artificially cropped inhalant siphon of *M. mactroides* at different seasons and levels of artificial severing to establish regeneration time in each condition.

MATERIALS AND METHODS

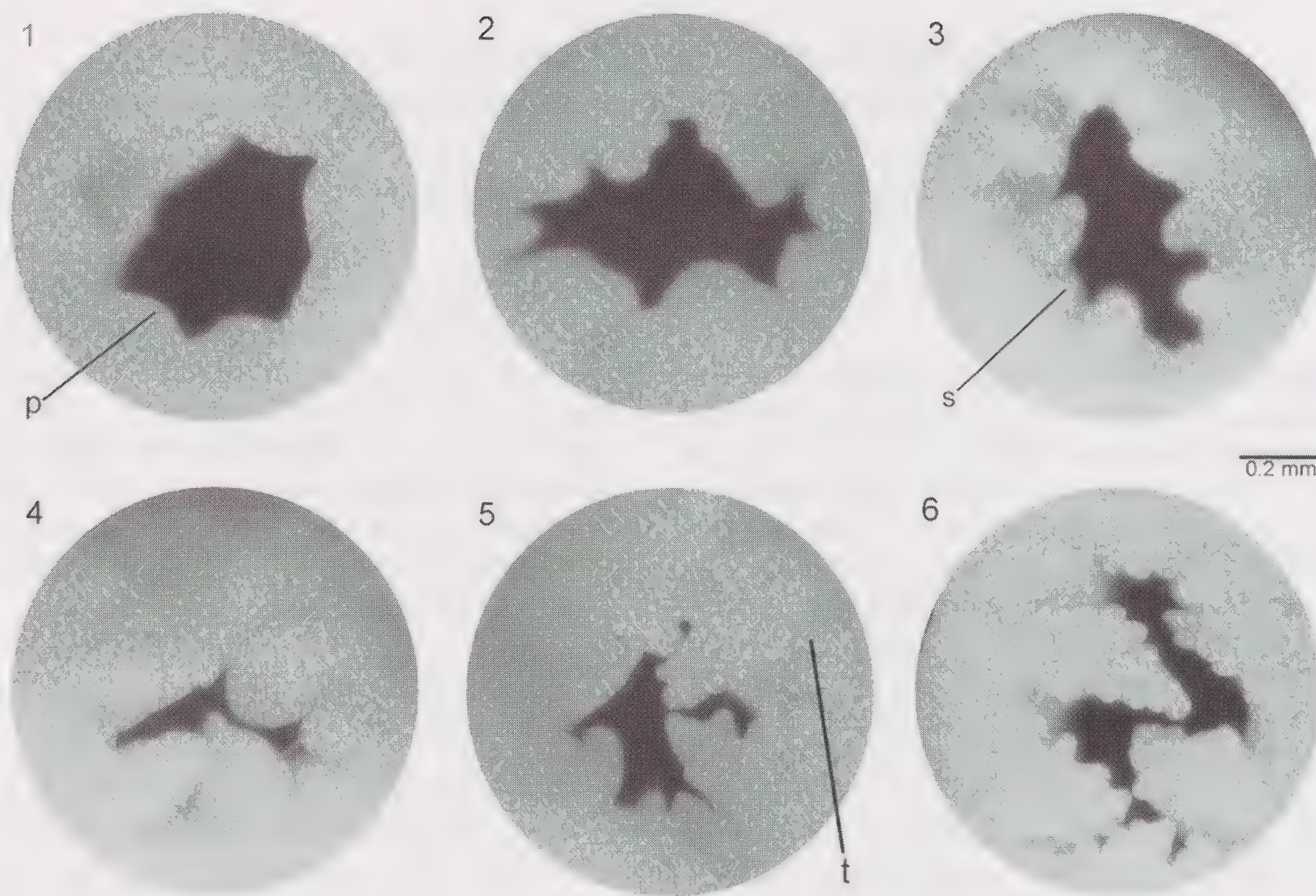
Individuals of *M. mactroides* were collected at Punta Mogotes beach, Argentina (37°59'S, 57°33'W). For a standardized of size range, only clams with shell length 4–6 cm were used. They were placed in 96 cm³ plastic aquariums with sand in an open system of unfiltered seawater. Before starting the experiments the animals were maintained for acclimation under these conditions for two days. In order to maintain a stable photoperiod characteristic of each season, artificial illumination was controlled. Water temperature was measured with an alcohol thermometer to the nearest 1°C and salinity with a refractometer to the nearest 1 ppm. The averages winter and spring temperature were 10.5 (± 2.9)°C and 15.7 (± 3.4)°C respectively. All systems simulated reported field densities of 577 individuals/m² (Bastida et al., 1991). To make the siphon nipping, the inhalant siphons were cut using surgery scissors after being placed in low oxygen sea water and relaxed with a solution of MgCl₂, following the procedure of Miloslavich et al. (2004).

Morphology of regenerating tentacle crown was studied on fixed tips (4% seawater formaldehyde) of nipped siphons under a stereoscopic microscope. The regenerating crown of two randomly chosen individuals was photographed each two days, during a 20-day period and then at day 30. Pictures were classified according to the regeneration degree

¹Laboratorio de Bio-Ecología de Crustáceos y Moluscos, Departamento de Ciencias Marinas, FCEyN, Universidad Nacional de Mar del Plata, Funes 3350, Mar del Plata 7600, Argentina

²CONICET, Av Rivadavia 1917 – CP C1033AAJ, Buenos Aires, Argentina

*Corresponding author: mcledon@mdp.edu.ar



FIGS. 1–6. *Mesodesma mactroides*. Sequence of regeneration of the tentacle crown during spring. primary tentacles (p), secondary tentacles (s), tertiary tentacles (t). FIG. 1: One day; FIG. 2: Two days; FIG. 3: Four days; FIG. 4: Six days; FIG. 5: Eight days; FIG. 6: Twelve days.

of siphons, as described in previous studies on the genus *Donax* (Miloslavich et al., 2004; Luzzatto & Penchaszadeh, 2001).

The primary tentacles were used as a parameter of siphon regeneration, because they grow until full regeneration. In the following experiments, the lengths of the 5 primary tentacles of two individuals of each group were measured (ten tentacles in total) under stereomicroscope each two days until the tentacles stop growing. To avoid the tentacles retraction, each individual was relaxed and inhalant siphon was cut thereafter.

Effect of Siphon Nipping at Different Cut-Levels

To study the effect of the level of cut on time and regeneration pattern, 80 yellow clams were divided into two groups. The distal 1 cm of the inhalant siphon was cut in one group and the distal 5 cm in the other. The clams were returned to the tank.

Seasonal Regeneration Rate

In order to compare differences in regeneration rate between winter and spring, the distal 1 cm of the inhalant siphon was cut to one group of 40 individuals in each season.

Effect of Laboratory Conditions

A field experiment was conducted in a plastic tank of 96 cm³ during spring. It was burrowed into the beach until flush with the sand and covered with a plastic net of 1-cm mesh size to prevent the escape of clams. The distal 1 cm of the inhalant siphon was cut to one group of 40 individuals.

Data Analysis

Data were analysed with repeated measurements ANOVA (rmANOVA). The principal effects were adjusted for sphericity violation using the corrections of Greenhouse-Geisser (G-G), Huynh-Feldt (H-F) y lower bound estimate (Lowr. Bnd). The results were analysed *a posteriori* with the test of Tukey.

RESULTS

In the winter experiment, clams developed the first rudiments of siphons at the first day after treatment. On the sixth day, the secondary tentacles started developing. On the twelfth day the tertiary tentacles started developing. In

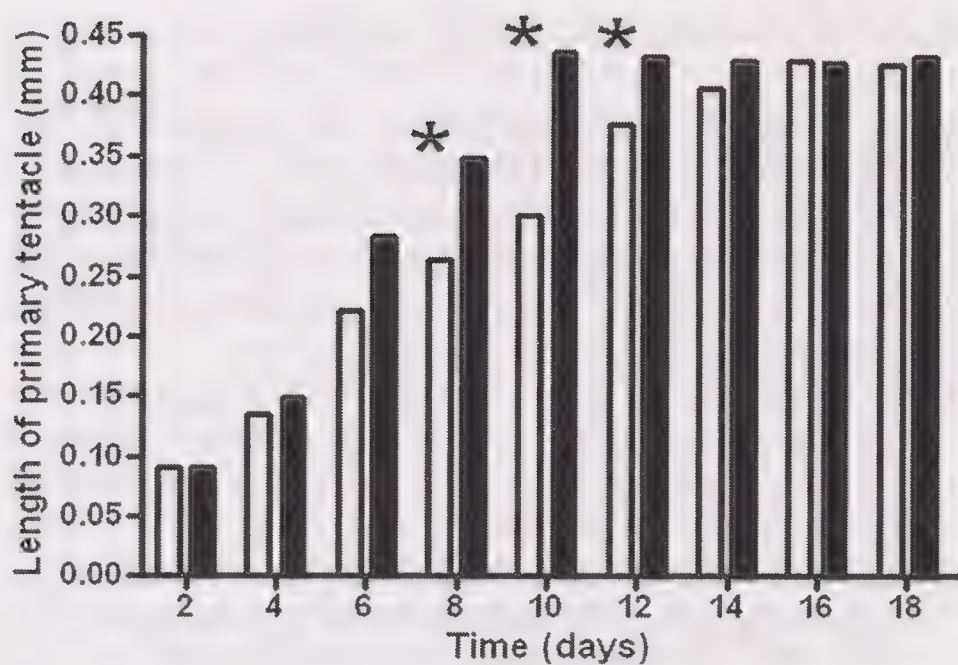


FIG. 7. Inhalant siphon of *Mesodesma mactroides*. Rate of regeneration of primary tentacles in different seasons. The black bars correspond to winter experiment and the white bars to spring experiment. Stars indicate statistical significant differences.

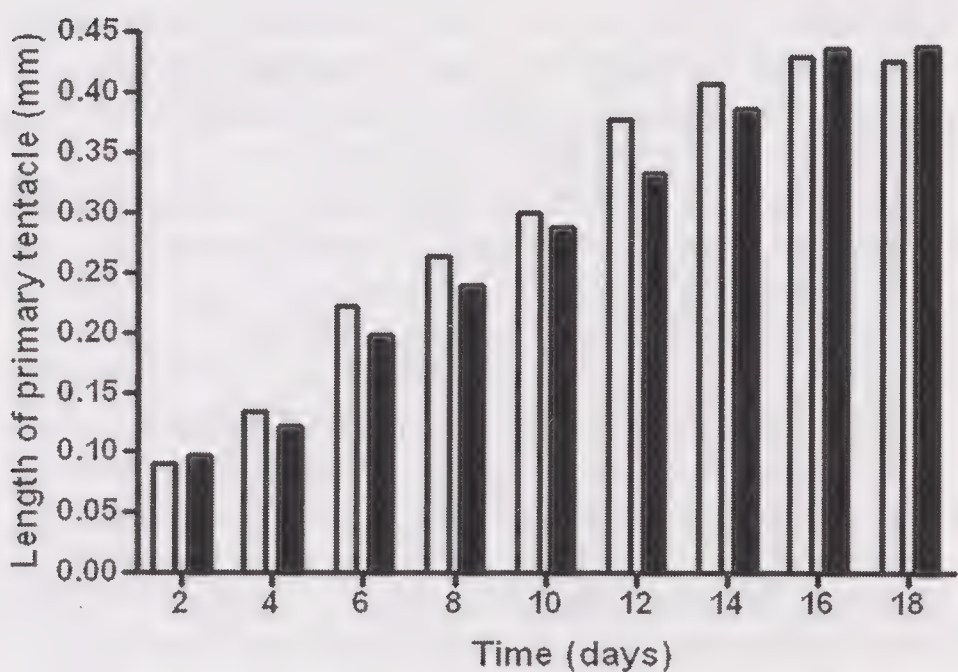


FIG. 8. Inhalant siphon of *Mesodesma mactroides*. Rate of regeneration of the primary tentacles in different levels. The black bars correspond to the individuals nipped at 5 cm and the white bars those nipped at 1 cm.

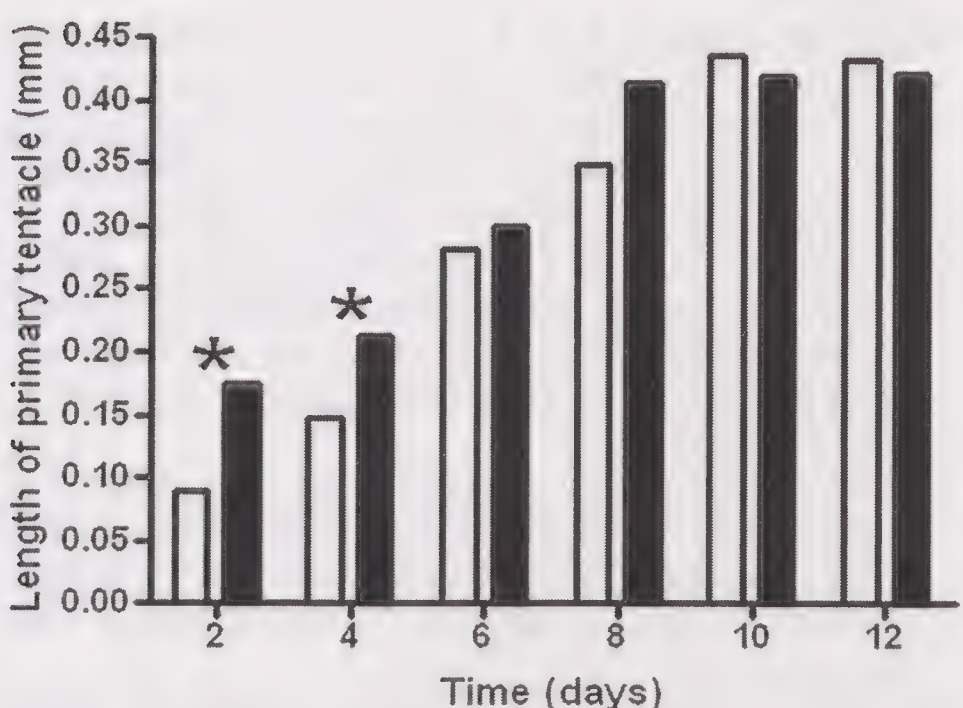


FIG. 9. Inhalant siphon of *Mesodesma mactroides*. Rate of regeneration of the primary tentacles in different experimental conditions. The black bars correspond to the laboratory experiment and the white bars to the field experiment. Stars indicate statistical significant differences.

spring, the regeneration took place faster than in winter. The first rudiment of siphon appear at the first day after treatment (Fig. 1), the secondary tentacles appeared six days after cutting (Fig. 3) (as in winter), but the tertiary tentacles eight days after that (Fig. 5). Figures 1 to 6 show the sequence of regenerations in spring.

Effect of Siphon Nipping at Different Cut-levels

No significant differences were found between treatments ($F = 1.67$; $df = 8$; $p > 0.05$).

Seasonal Regeneration Rate

Significant differences were found between winter and spring treatments ($F = 9.19$; $df = 5$; $p < 0.05$), and the test of Tukey showed different spread from the eight day until the end of the experiment.

Effect of Laboratory Conditions

Significant differences in tentacle length of spring field and laboratory treatments were found ($F = 7.66$; $df = 5$; $p < 0.05$). The test of Tukey also demonstrated significant differences as early as the fourth day, showing a faster growth in the laboratory experiment than in field experiment.

DISCUSSION

The regeneration process started a day after the ablation of the distal end of the inhalant siphon, when the primary tentacles initiate their development. The most dramatic events in the regenerating process of the inhalant siphon were detected within the first 96 hours after the treatment, with fast regeneration of primary and secondary tentacles, whereas the regeneration of tertiary tentacles delayed until the twelfth day in winter and eighth day in spring. Therefore, primary and secondary tentacles must play a more important role in providing basic functionality to the siphon. The slow process of regeneration observed within the first day after ablation of the tentacle crown occurs probably due to the malfunctioning of the siphon addition the physiological adequation needed for the tissue reparation, therefore limiting the food and oxygen intake of individuals with removed tips.

The regeneration time registered during both season experiments was longer than that reported by Luzzatto & Penchaszadeh (2001) for *Donax hanleyanus*, Miloslavich et al. (2004)

for *D. denticulatus*, and Pekkarinen (1984) for *Macoma balthica*.

The time in the regeneration process of the primary tentacles was related with the season (Fig. 7). Similar results were found in *Nuttallia olivacea* by Tomiyama & Kinuko (2006). This could be explained by the higher temperatures in spring, which accelerates the process or a higher food intake due to spring algal blooms. The rate of regeneration in *M. mactroides* was independent of level of siphon ablation (Fig. 8).

In the field experiment, the total time required to complete regeneration was similar to that under laboratory conditions, but in the former case, the process started sooner (Fig. 9). The rapid initial tentacular growth in field conditions suggests a reallocation of energy to crown formation. The delay in the regeneration start in the laboratory experiment probably was due to some non-simulated environmental variable, such as wave frequency.

This optimizes filtration, which would be of high energetic cost for the individuals of the field experiments due to the amount of suspended matter to filter.

Siphon loss reduces burrowing depth (Zwarts & Wanink, 1989; Zwarts et al., 1994; de Goeij et al., 2001; Meyer & Byers, 2005), increasing the risk of lethal predation by crabs or shorebirds, and decreasing feeding activity (Peterson & Skilleter, 1994; Skilleter & Peterson, 1994; Zwarts et al., 1994; de Goeij & Luttikhuisen, 1998). Rapid siphon regeneration is probably necessary for bivalves to attain sufficient reburial depth as soon as possible (de Goeij et al., 2001). In *M. mactroides*, siphon nipping reduces the deep of burrowing increasing the mortality by predation (Cledón et al. submitted), as reported in the bibliography in other bivalves (Haddon et al., 1987; Smith et al., 1999; Whitlow et al., 2003). So the clams would need to regenerate the tentacle crown to improve filtration optimising the available energy for recovering the normal deep of burrowing.

In this study was observed that individuals belonging to the same clam population increased the regeneration rate from winter to spring. It is still to be tested if these rate influences in the time that the clams remain exposed predators.

ACKNOWLEDGMENTS

The present work was partially supported by the Sophie Danford Foundation and PICT2007-01398. We would like to thank Dr. P. E. Penchaszadeh and Dr. R. Bastida for their invaluable comments during the preparation of the experiments.

LITERATURE CITED

- BASTIDA, R. A., A. ROUX, C. BREMEC, M. GERPE & M. SORENSEN, 1991, Estructura poblacional de la almeja amarilla (*Mesodesma mactroides*) durante el verano de 1989 en la provincia de Buenos Aires, Argentina. *Frente Marítimo*, 9A: 83–92.
- CASTELLANOS, Z. J. A. De, 1970, Catálogo de los moluscos marinos bonaerenses. *Anales Comisión de Investigaciones Científicas de la Provincia de Buenos Aires*, 8: 1–365.
- CLEDÓN, M., J. D. NUÑEZ & M. A. SCHELZO, Siphon nipping facilitates lethal predation in the clam *Mesodesma mactroides* (Reeve, 1854) (Mollusca: Bivalvia). *Marine Biology*, submitted.
- DE GOEIJ, P. & P. LUTTIKHUIZEN, 1998, Deep-burying reduces growth in intertidal bivalves: field and mesocosm experiments with *Macoma balthica*. *Journal of Experimental Marine Biology and Ecology*, 228: 327–337.
- DE GOEIJ, P., P. C. LUTTIKHUIZEN, J. VAN DER MEER & T. PIERSMA, 2001, Facilitation on an intertidal mudflat: the effect of siphon nipping by flatfish on burying depth of the bivalve *Macoma balthica*. *Oecologia*, 126: 500–506.
- GELLER, J. B., 1990, Reproductive responses to shell damage by the gastropod *Nucella emarginata* (Deshayes). *Journal of Experimental Marine Biology and Ecology*, 136: 77–87.
- HADDON, M., R. G. WEAR & H. A. PACKER, 1987, Depth and density of burial by the bivalve *Paphies vermicosa* as refuges from predation by the crab *Ovalipes catharus*. *Marine Biology*, 94: 25–30.
- HODGSON, A., 1982, Studies on wound healing and regeneration of the siphon of the bivalve *Donax serra* (Röding). *Transactions of the Royal Society of South Africa*, 44: 489–498.
- IRLANDI, E. A. & M. E. MEHLICH, 1996, The effect of tissue cropping and disturbance by browsing fishes on growth of two species of suspension-feeding bivalves. *Journal of Experimental Marine Biology and Ecology*, 197: 279–293.
- KAMERMANS, P. & H. J. HUITEMA, 1994, Shrimp (*Crangon crangon* L.) browsing upon siphon tips inhibits feeding and growth in the bivalve *Macoma balthica* (L.). *Journal of Experimental Marine Biology and Ecology*, 175: 59–75.
- LUZZATTO, D. & P. E. PENCHASZADEH, 2001, Regeneration of the inhalant siphon of *Donax hanleyanus* Philippi 1847 (Bivalvia, Donacidae) from Argentina. *Journal of Shellfish Research*, 20(1): 149–153.
- McLACHLAN, A., E. JARAMILLO, O. DEFEO, J. DUGAN, A. DE RUYCK & P. COHETES, 1995, Adaptations of bivalves to different beach types. *Journal of Experimental Marine Biology and Ecology*, 187: 147–160.
- MEYER, J. & Y. J. E. BYERS, 2005, As good as dead? Sublethal predation facilitates lethal predation on an intertidal clam. *Ecology Letters*, 8(2): 160–166.
- MILOSLAVICH, P., P. E. PENCHASZADEH, A. K. CARBONINI & D. SCHAPIRA, 2004, Regeneration time and morphology of the inhalant siphon of *Donax denticulatus* Linneé, 1758 (Bivalvia,

- Donacidae) after amputation. *Journal of Shellfish Research*, 23(2): 447–450.
- NARCHI, W., 1981, Aspects of the adaptive morphology of *Mesodesma mactroides* (Bivalva: Mesodesmatidae). *Malacologia*, 21: 95–110.
- PEKKARINEN, M., 1984, Regeneration of the inhalant siphon and siphonal sense organs of brackish-water (Baltic Sea) *Macoma balthica* (Lamellibranchiata, Tellinacea). *Annales Zoologici Fennici*, 21: 29–40.
- PENCHASZADEH, P. E., 1983, Sub-tidal sandy beach trophic structure in the area of Punta Morón, Venezuela. Pp. 523–528, in: A. McLACHLAN & T. ERASMUS, eds., *Sandy beaches as ecosystems*. Junk, The Hague, The Netherlands, viii + 757 pp.
- PETERSON, C. H. & M. L. QUAMMEN, 1982, Siphon nipping: its importance to small fishes and its impact on growth of the bivalve *Protothaca staminea* (Conrad). *Journal of Experimental Marine Biology and Ecology*, 63: 249–268.
- PETERSON, C. H. & G. A. SKILLETER, 1994, Control of foraging behavior of individuals within an ecosystem context: the clam *Macoma balthica*, flow environment, and siphon-cropping fishes. *Oecologia*, 100: 256–267.
- RIERA, A. A., 1995, Relaciones tróficas interespecíficas en una comunidad íctica de una playa arenosa del estado Falcón. Universidad Simón Bolívar, Trabajo Especial de Grado, 63 pp.
- SKILLETER, G. A. & C. H. PETERSON, 1994, Control of foraging behavior of individuals within an ecosystem context: the clam *Macoma balthica* and interactions between competition and siphon cropping. *Oecologia*, 100: 268–278.
- SMITH, T. E., R. C. YDENBERG & R. W. ELNER, 1999, Foraging behaviour of an excavating predator, the red rock crab (*Cancer productus* Randall) on soft-shell clam (*Mya arenaria* L.). *Journal Experimental Marine Biology and Ecology*, 238: 185–197.
- TOMIYAMA, T. & I. KINUKO, 2006, Regeneration of lost siphon tissues in the tellinacean bivalve *Nuttallia olivacea*. *Journal of Experimental Marine Biology and Ecology*, 335: 104–113.
- TREVALLION, A., R. EDWARDS & J. H. STEEL, 1970, Dynamics of a benthic bivalve. Pp. 285–295, in: J. H. STEELE, ed., *Marine food chains*. Oliver & Boyd, Edinburgh, U.K., viii + 552 pp.
- TREVALLION, A., 1971, Studies on *Tellina tenuis* (Da Costa). III. Aspects of general biology. *Journal of Experimental Marine Biology and Ecology*, 7: 95–122.
- WHITLOW, W. L., N. A. C. RICE & C. SWEENEY, 2003, Native species vulnerability to introduced predators: testing an inducible defense and a refuge from predation. *Biological Invasions*, 5: 23–31.
- ZWARTS, L., 1986, Burying depth of the benthic bivalve *Scrobicularia plana* (da Costa) in relation to siphon-cropping. *Journal of Experimental Marine Biology and Ecology*, 101: 25–39.
- ZWARTS, L. & J. WANINK, 1989, Siphon size and burying depth in deposit and suspension-feeding benthic bivalves. *Marine Biology*, 100: 227–240.
- ZWARTS, L., A. M. BLOMERT, P. SPAAK & B. DE VRIES, 1994, Feeding radius, burying depth and siphon size of *Macoma balthica* and *Scrobicularia plana*. *Journal of Experimental Marine Biology and Ecology*, 183: 193–212.

Revised ms. accepted 4 October 2009